A CONTRIBUTION TO THE NATURAL HISTORY AND DEVELOPMENT OF PENNARIA TIARELLA McCr.

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I. Introductory.

The observations of which the following paper is a summary have been carried on during three summers at the Marine Biological Laboratory, and in part at the laboratory of the United States Fish Commission, from the directors of which I am very glad to acknowledge many courtesies and facilities for prosecuting the work.

The circumstances attending the work have been so varied during the years of its continuance that it may be hoped most of the errors liable to hasty observation have been avoided, and to a considerable measure the error liable to the personal equation of prepossession, where time is not allowed for its elimination.

Pennaria tiarella McCr. was first described by Ayers ('**52**), under the name of *Globiceps tiarella*, who has summarized its generic characters in substance as follows: Polypodon rising from a creeping root, branched. Short stems from the branches, supporting each a single polyp. Polyps encircled by three rows of arms, basal, median and near summit; the arms of the upper rows ending in globular heads. Polyp not retractile in tube. The name of the genus, Globiceps, from the peculiar form of the arms. The specific name from the number of the rows of arms. He gives no account of its distribution, except to mention that it has been taken at Sag Harbor and in Boston Harbor. Of its habitat he merely mentions that it occurs on fucus or similar substratum.

It was later described by Leidy ('**55**), under the name of *Eucoryne elegans*. McCrady ('**57**) was the first to recognize its true affinities with the Pennaridæ and designated it by the

name under which it is now known. L. Agassiz early pointed out nomenclatural objections to the name Globiceps of Ayers, and Eucoryne of Leidy, and at the same time indicated certain differences between the diagnostic characters of this hydroid and those originally designated as distinctive of the genus by Cavolini and Goldfuss. A. Agassiz ('65) in the catalogue of the North American Acalephæ has, however, followed the designation of McCrady, and has in turn been followed by most American students of the Hydroidea.

Still later, however, Allman ('71) took up the suggestion of the elder Agassiz concerning the unavailability of the generic terms Globiceps and Eucoryne and, discrediting the contention of McCrady as to the identity of the form with that of Pennaria, proposed the new generic name Halocordyle. He bases his claim for such distinction wholly upon the apparent difference as to the arrangement of the arms, or tentacles, those of the hydroid under consideration being distributed in verticillate whorls about the hydranth, while those of *Pennaria gibbosa* have them somewhat promiscuously distributed over the body of the polyp.

It might be sufficient warrant for doubt as to Allman's contention that his diagnosis is based chiefly upon published figures of the hydroid, having in neither case had access to living specimens. And when added to this there is recognized the further fact that a careful study of several species from different regions, and from the same region, shows all degrees of intergradation in these respects, an unhesitating dissent from Allman's view will not be regarded as extravagant.

II. MATERIAL AND METHODS.

The material chiefly used was obtained at Woods Holl during the summers of 1897, 1898, and 1899, and in almost unlimited quantities. Material of P. Cavolini was secured and preserved by the writer from the Bay of Naples in 1894, and was used in many points of comparison, as will be indicated in appropriate phases of the paper. In general, collections were made at low tide and in the waters in and about the harbor,

from eelgrass, piles of the Fish Commission docks, and from fucus and rocks in the shallowed waters in and about the rocky outlet of the "hole." Material specially for the developmental work was usually collected, when convenient, during the later afternoon, so that no considerable time should elapse before the discharge of the eggs. When by reason of tides this was not practicable, collections were made at other hours, and the material placed in floats off the exposed sides of the docks, where conditions of water, temperature, etc., would be as nearly normal as possible. Experiments, however, showed that this precaution was not essential, no apparent differences being distinguishable between collections brought to the laboratory aquaria and those floated outside.

For killing and fixing, many methods were tried, but without that marked preferential distinction for one or a few which is often found for other material. Almost any of the standard fixing agents will give fairly good results. If any preference is assignable, I should give it to the stronger solutions of Kleinenberg's picro-sulphuric acid, or picro-acetic, in which the acetic acid was often used in a solution as strong as 10 per cent. The various corrosive solutions gave results of about equal value, and for carmine staining was specially good. Perenyi's fluid gave fairly good results, though less certain than the others. Flemming's fluid, while affording admirable fixation, rendered subsequent staining so difficult as to make its value secondary.

For surface study of the eggs, out of a very large number of experiments with numerous staining agents, only one gave results of sufficient value to be worth record, namely, Conklin's picro-sulphuric-hæmatoxylin, and this, when compared with results upon such eggs as those of Mollusca, was quite inferior, though enabling one to distinguish definitely considerable of the internal organization of the egg from surface views. In no other egg, save that of Eudendrium, have I found such difficult material from which to secure even approximately good differential staining reactions. Whether this is due to some physiological condition peculiar to these eggs, or to their peculiar opacity, I am unable to say.

III. NATURAL HISTORY.

Pennaria tiarella is one of the most abundant and beautiful hydroids to be found in the waters of the northeastern Atlantic coast, occurring abundantly in tide pools, upon piles of docks, fucus, etc. Its generic name indicates one of its most conspicuous features, namely, the feather-like form of the main stem and its branches, which spring laterally and alternately from either side. When growing in dense tufts or colonies this feature is often obscured in a measure or, in some cases, even lacking entirely. In size it varies greatly as found under varying conditions of environment. Under the best conditions it may have a height of six inches or even more, while under circumstances less favorable it may scarcely have a height of more than two inches.

In this connection may be noted a rather interesting and, so far as I know, an unrecorded peculiarity of habitat, namely, its occurrence during the summer under apparently two conditions, the one appearing considerably earlier and finding a habitat, as already indicated, upon rockweed, piles, etc., the other occurring later and in great abundance upon eelgrass. The latter form rarely attains the larger size given, but it matures with much greater rapidity and has apparently a much briefer period of activity, hardly covering more than about four or five weeks. It is further distinguished by a higher coloration of the colonies and the medusæ. Again, the medusæ free themselves with much greater frequency and ease, and swim much more actively. The ova of the two forms likewise show the same difference of coloration, those of the latter being a brighter orange and much more conspicuous, while those of the former are of a creamy white, with the slightest tint of dull pink.

Morphologically these forms exhibit no constantly distinctive differences. The first, from its habit in usually deeper water, and thus constantly submerged condition, does not exhibit that marked feather-like bilateralism common in the eelgrass form, which, from the fact that it often floats upon the surface and, at low tide, often lies quite exposed, would come naturally to assume the bilateral form. This fact may likewise account in

part for the higher coloration exhibited by the latter, and might naturally occasion the more rapid development of the colonies, as well as the greater activity of the medusæ, since their exposure at low tide and always near the surface would give them the advantage of the naturally higher temperature of the surface water. May it not be probable that this condition is an adaptive one for the more rapid multiplication of the sexual persons which, by their greater activity, secure a greater distribution? For it must be noted that the medusæ of the deep-water forms are much less active, in many cases never becoming free at all, and when becoming so rarely swimming actively. During one entire season I failed to detect this feature which I have since found to be a very common one. At one time I was inclined to suspect that, as McCrady had suggested (**'57**), the ova might have developed within the bell of the medusæ and emerged as planulæ, for, in more than one collection brought in during the early morning, numbers of planulæ were found among the fucus-bearing hydroids, and among the stems of the colonies themselves, while the yet living medusæ were found still attached to the hydranths. McCrady's observations may have been due in part to the fact that in many cases these deeper water medusæ do not seem to discharge the ova freely, and, since the free exposure of the ova within the bell of the medusa insures usually their fertilization, so, as a matter of course, the development follows without interruption. It is more probable, however, that his observations were due to a misinterpretation of the singular phenomena of segmentation, to be described later.

After the discharge of the ova the medusæ, when free, continue to swim about actively for a time, but soon begin to show signs of decline and rarely live beyond a few hours, sometimes twelve or even twenty-four, though A. Agassiz has recorded their living in confinement for several weeks. My own observations, however, show no confirmation of this. They rather confirm the observations of McCrady, who remarks upon the "apathetic condition of the medusa, following the expulsion of the planules."

In common with most hydroids Pennaria is distinctively a

summer organism, at least in its actively vegetative condition. I have not found records of its occurrence in flourishing condition later than November, and during several years of observation have not taken it in mature form earlier than June, though its seasonal variation may be considerable. After its more active period there is an evident decline in vigor, and later a degeneration of the polyps and hydrocaulus, and a recession of the cœnosarc within the stoloniferous hydrorhiza, followed by a period, more or less prolonged, of quiescence. This is chiefly a seasonal peculiarity, induced doubtless by coincident changes of temperature, food, etc. It may occasionally, however, be induced by conditions purely local and temporary. Colonies now and then show an evident decline for a period of varying extent and then may revive and regain their normal activity within a few weeks. In these cases no discernible cause is evident, and hence they have been designated as purely local and temporary.

Pennaria exhibits in a very marked way the phenomenon of "alternation of generations." The nonsexual, or vegetative, phase comprises the splendid hydroid features whose natural history has now been outlined. Its sexual, or medusa, phase presents an organism which Agassiz ('65) has characterized as "one of the most remarkable of our naked-eyed medusæ." In form it is elongate-oval, slightly smaller at the oral end. In Pl. I, Figs. 2 and 3, are shown adult medusæ with developing and mature eggs. Its size varies slightly, but averages about 1.5 mm. in length, and .8 mm. in short diameter.

In its natural history the medusa exhibits some very interesting features. Some of these have already been pointed out, such as the variation in coloration, activity, etc. Smallwood ('99) has observed in working out its development evidences of degenerative conditions which harmonize with some of the observations previously cited, and with similar conditions among not a few other of the Hydromedusæ, *e.g.*, Clava, Hydractinia, etc.

The medusæ mature with comparative rapidity and show a rather marked periodicity as to the time of liberation. And here again there is a rather sharp difference between the so-

called eelgrass forms and those of the deeper water habit. The former are liberated usually from about 7 to 8 P.M., followed almost immediately by the discharge of the sexual products. In the latter form the time of liberation varies from about 10 to 12 P.M. In each case the male medusæ are, as a rule, first set free, usually from a few minutes to half an hour. Fertilization of the eggs occurs at once upon their discharge.

In Pl. I, Fig. 2, is shown a mature medusa as it appears within a few hours of its liberation from the hydroid. At this time the nearly mature ova occupy almost the whole interior of the bell, often distorting in some measure its form. In no case, however, have I observed any such remarkable distortion at this stage as that described and figured by Agassiz ('65), and I am disposed to suspect that his specimen must have been a very unusual one, for certainly with ova surrounding the whole of the manubrium and compressing it greatly a one-sided distortion must be rather difficult to understand. As the ova grow about the manubrium they are flattened, disk-shaped bodies of an outer convex and an inner concave aspect. Approaching maturity they begin to assume a more or less spherical form, as indicated in the figure. Just prior to the release of the medusa, and perhaps induced in part by the rhythmic contractions by which this is effected, they assume a perfectly spherical form; the mesenterial membrane becomes more closely fitted to each individual egg, and at the moment of release the animal has the form exhibited by Pl. I, Fig. 3. Swimming rapidly about with the characteristic jerking movements common to these smaller medusæ, the ova are discharged one by one as the animal swims, and thus a considerable distribution is secured to the ova and the new colonies to arise from them. In the growth and maturity of the male medusa essentially the same phenomena are exhibited. The sperms closely pack the whole subumbrella cavity, but as the medusa is about to be liberated the mesentery seems to contract, and quickly following this, as release is effected, the membrane is ruptured and the sperms discharged in immense numbers.

IV. Maturation and Fertilization.

Under these heads I shall give at this time only the merest synopsis of my observations, for there are many points yet to be worked out in detail, and to these I shall give special attention in a later paper, which is, however, well under way and may, I trust, appear within the near future.

As Smallwood has pointed out ('99), and as Doflein ('96) has also shown for Tubularia, and as I have found in Parypha, the ova grow within an ovarian mass of primitive ova by the consumption of their fellows, nuclei of which may be seen in all stages of degeneration, both about and within the growing eggs. In Parypha the most perfect illustrations of degenerative metamorphosis and amitotic division are shown, and in this form they are not wholly disintegrated during the process of segmentation of the egg, nor even till after at least the ectoderm of the larva is very clearly established.

As the egg grows the nucleus migrates toward the periphery, becomes very indefinite in form, and also seems quite indifferent to ordinary staining processes. In only a few cases have I found from surface preparations, and in observations upon the living egg, any clear examples of polar bodies. However, the fact that the ova are devoid of membrane and are peculiarly opaque would naturally obscure or render quite transient these bodies. The ova are of relatively large size, varying from .4 mm. to .5 mm. in diameter, and heavily yolk-laden, and, as already indicated, vary in color from a creamy white with faint trace of pinkish hue to a clearly orange color.

Fertilization occurs very soon after the ova are discharged from the medusa, and hence only external, unless, as indicated in another part of the paper, where, after the velum is ruptured as well as the mesentery suspending the egg, fertilization may readily take place within the bell cavity. A number of experiments and observations have demonstrated this quite conclusively. Artificial fertilization is quite easy and can be controlled at will. Very soon after extrusion of the egg, sperms may be seen surrounding it in great numbers, in some cases completely covering it and adhering for some time. The

entrance of the sperm produces a profound effect upon the egg, which up to that time has been quite passive. Examined under a low power the egg very soon after access of the sperm shows a sort of convulsive surface torsion, which after a few minutes quite disappears, and the egg again becomes quiescent. But within half an hour, often sooner, the phenomena of cleavage begin and usually go forward with comparative rapidity, the entire process, so far as surface features are concerned, becoming complete within a few hours, though varying greatly in different eggs and under slight differences of temperature.

V. Cleavage.

Of cleavage phenomena in Pennaria it is extremely difficult to formulate an account, and that for several reasons. A glance at the figures which present only some of the more striking aspects of the subject will afford one, and perhaps a sufficient, reason. Again, the unusual opacity of the eggs renders difficult, either in the living or preserved material, any critical insight into other than the surface phenomena. There seems to be no law or order attending the process. Every egg is a law unto itself and is absolutely indeterminate as to order or rate of development. Beyond the accounts of Wilson for Renilla ('84), and Metschnikoff for Ratkea and Oceania ('86), the literature at my command affords nothing comparable, and these are only remotely so. Andrews ('98) points out "Some Ectosarcal Phenomena in the Eggs of Hydra," which, while in some features they are similar to some aspects associated with these phenomena in Pennaria, seem yet to be of a decidedly different character. Similar ectosarcal features were more or less obvious in the eggs of Pennaria, bits of protoplasmic matter at times being extruded and even detached from the surface of the egg, including at times considerable portions. Again, the presence of more or less definite protoplasmic bands, or bridges, during the earlier phases of cleavage is a very conspicuous feature in Pennaria. That it may in some way be associated with fertilization, the entrance of several Spermatozoa, artificial conditions, or otherwise, would seem not improb-

able. The highest powers of the microscope revealed nothing which seemed quite comparable with the so-called spinning movements of protoplasm, to which Andrews has directed attention.

So anomalous are these phenomena that during the first several series of observations the conclusion was unavoidable that they were strangely abnormal or, perhaps, pathologic. Accordingly, the first series were wholly discarded, except a few specimens which had been isolated in watch glasses and set aside more out of curiosity than otherwise, and left overnight. An inspection the following morning revealed several apparently normal larvæ. The observations of the following night were to the same effect, though at this time a considerable series of all sorts were isolated with pains to eliminate possible error, and with results quite assuring, in that in a very large proportion of the cases perfect larvæ resulted and continued to develop. Following this, systematic collections were made and painstaking observations and records kept of every feature associated with development.

Occasionally an egg would segment with a fair degree of regularity into the two, four, and eight cell stage, as shown in Pl. II, Figs. 7, 8. But beyond this point it was difficult to follow any order in the cleavage, though it might continue with more than ordinary regularity as compared with the average of its fellows. It was utterly impossible to trace anything like a definite lineage of cells, notwithstanding repeated and careful attempts. By no means was it possible to predict the direction or course or rate of any division beyond the first or second phase of the cleavage, and even then only occasionally.

While Wilson ('84) has noted a considerable degree of individual variation in the cleavage of Renilla, he is still able to reduce it to some half dozen types. With Pennaria, however, while it is possible to recognize some few rather predominating types in the earliest cleavage, as, for example, a centripetal, a centrifugal, and a vertical, yet they are not of sufficiently pronounced character to constitute well-defined types which are distinguishable as such. In no case were there any clearly defined and symmetrical equatorial phases recognizable, though

occasionally incipient aspects of it were detected. This may be due in part to the membraneless condition of the eggs, but perhaps rather to their more or less evident amœboid condition, which asserted itself in the earlier phases. Again, the eggs early became somewhat flattened and disk-shaped, and only as the external phenomena of cleavage were completed did they resume an approximately spherical form. In Pl. II, Figs. 1–6, are shown a single series of cleavage phases noted at intervals of ten minutes or less. All were sketched from life by the aid of a camera, and, as will be noted also, there are presented only the *earlier* phenomena. As segmentation progressed its superficial aspects became less and less evident, owing to the opacity of the eggs, and only in a few cases were attempts definitely made to follow it to anything like completion. In these and other figures will readily be recognized the amœboid aspects referred to above.

Reference has been made incidentally to the variable rate of segmentation. This feature was quite as marked as were others, both as to individual eggs and blastomeres. In many cases a single blastomere would divide at a rate quite phenomenal, so that it was difficult to sketch adequately successive phases, while others might remain in a state of inaction for an indefinite period or even be engulfed bodily into the more rapidly segmenting portion. Then, also, in many cases cleavage seemed to begin in a somewhat discoidal fashion at a single pole and only gradually extend to other portions, as shown in Pl. IV, Fig. 1. This could hardly be due to any marked inequality in the distribution of the food yolk, for in this respect the eggs of Pennaria seem to be quite isotropous, and indeed there seems little if any definite polarity of any sort evident in these eggs. Occasionally, as shown in Pl. IV, Fig. 1, cleavage appeared to advance from a single area, but in the large proportion nothing of the sort was evident, and, as Conklin ('97) has shown in molluscan eggs, where the greatest variation in matter of yolk distribution is distinguishable, there is none the less a perfect symmetry of rate and character of cleavage. This would seem to be only another illustration of the inadequacy of any known law as an explanation of all cleavage phenomena.

That these are really cleavage, and not merely amœboid phenomena, can hardly be matter of serious doubt, even when considered from the more superficial phenomena already presented. If, however, other evidence were needed, it is available in the greatest profusion from sectional sources, portraying the internal structure and organization of the egg. In Pl. IV, Figs. 1–6, are shown camera sketches, of a few sections only, of eggs in different stages of segmentation. That they are clearly correlated in general features with the superficial features already noted there is no doubt whatsoever, though there may be many points of detail which need attention, but which can only be touched upon at this time. That Pl. IV, Fig. 2, is comparable with that of Pl. II, Fig. 7, as a two-cell stage must be obvious at a glance. There are, however, here some interesting facts to which a moment's consideration may be directed. It will be seen, for example, that there are present, in the section, portions of several nuclear figures, a somewhat unusual condition at this stage of development. However, here again there is something in common with what Wilson has recorded in certain cases in Renilla, namely, the internal nuclear division preceding that of the cytoplasm which followed, or lagged, as it were, finally dividing at once into an equal number of cells. It is, however, quite different in that in these the nuclear cleavage seems constantly to outrun that of the cytoplasm. It had occurred to me that possibly there might be here what has been noted by Loeb ('99), Norman ('96), and others, namely, a sort of artificially produced cleavage of the nucleus, induced by some chemical or pathological stimulus. The comparison of many sections, preserved under different conditions, and by different methods, however, leads me to conclude that it is a perfectly normal condition so far as these particular eggs are concerned. I have also observed the same thing in the eggs of other hydroids, and Hickson ('93) calls attention to a similar condition in the cleavage of Allopora. It would seem as if from some cause, not perhaps easily distinguishable, that all the phenomena of cleavage in some of these organisms have been greatly modified, that in some way the nucleus and cytoplasm have, as it were, been thrown out of concord, and their

rhythmic relations disturbed to such an extent that this very erratic and anomalous type of segmentation has resulted. May it not be within the line of possibilities that the peculiar methods and conditions of growth and maturation of these and some similar eggs have in some way been the occasion of the disturbance? While only a suggestion, yet it seems not without the range of possibilities.

In Pl. III, Figs. 1–7, are shown conditions not uncommonly met with, which are specially interesting in that from one such were derived spontaneously two perfect embryos, a fact, so far as I am aware, quite unusual, if not unique, though Metschnikoff ('86) cites a somewhat similar case in the development of *Oceania armata.* It does not seem clear, however, from his account whether the cases are quite similar, certainly not in the details of the cleavage. Following the first cleavage in these eggs, during which the blastomeres become widely separated, the two halves proceed to develop quite independent of each other and show no disposition to reunite until the cleavage is quite advanced, apparently to the point of completion or nearly so, when usually they gradually approximate and finally fuse into a typical morula and develop into a normal embryo. In at least one case a specimen which showed this aspect in a very marked degree at an early stage gave rise to two perfect larvæ, though of small size. The specimen was carefully isolated in a large watch glass and set aside as a test case, and the next morning the larvæ were found in perfect condition, as indicated. Several others of similar character were subsequently isolated in the same way, but in only the one case did this spontaneous division show itself conclusively. That such cases, though rare, are not strange among these organisms may be very well conceded, specially when the peculiar phenomena associated with the early development are familiar.

VI. Completion of Segmentation and Formation of the Planula.

Following the more conspicuous and anomalous aspects already considered, the egg gradually assumes a nearly spher-

ical form, hard to distinguish from the freshly discharged ovum, almost all surface aspects of cleavage having disappeared. In this form it remains apparently quiescent for some hours, during which time, however, internal cell division goes on quite actively, as sections clearly show. With completion of this internal cleavage the embryo becomes a solid morula, with only the faintest indications of any differentiation into an ectoderm (*cf.* Pl. IV, Fig. 6). Following this, however, the specialization of an ectoderm soon takes place, and the embryo begins to assume the characteristic pyriform, or oval, shape of hydroid planulæ. Within from twelve to twenty hours cilia make their appearance over the ectoderm, and the free life of the larva is assumed. Up to this time, however, and for some time after, no definite endoderm has been formed; the entire mass of internal cells seem scarcely distinguishable from each other, except that near the central portion the remains of yolk débris are more or less apparent. It is not till after some hours of larval life that an endoderm is gradually specialized from the internal cell mass and takes on an appearance quite similar to that of the forming ectoderm. After the establishment of the diploblastic condition there still remain a mass of undifferentiated cells, intermingled with yolk granules, which seem gradually to disintegrate and are consumed as food by the developing larva, which, up to the polyp stage, is wholly without mouth or other means of taking solid food, though in all probability absorption of water with soluble matter in small proportion takes place.

The larval history of Pennaria seems considerably longer than the corresponding period of many other hydroids. In several cases specially noted the planulæ did not settle for attachment and transformation till some five days following the beginning of development, and only at the end of seven days were tentacles well marked, as shown in Pl. III, Fig. 10. The tentacles originate by a process of budding, the lower, or filamentous, series appearing first, those of the other series following somewhat later.

Secretion of the perisarc begins almost at once after the attachment of the larva, preliminary to transformation. At

first it is an exceedingly delicate, almost indistinguishable, transparent film about the base of the polyp. This gradually thickens and soon hardens into a sheath about the growing polyp, covering at first the entire larva. Annulation of the perisarc seems to occur at no very definite time or place in its growth. In some cases it is apparent almost from the first. In others it only becomes apparent at a considerably later time, and nearer the hydranth than the base. As to the significance of the annulations, either in origin or function, nothing very definite can be said. That the perisarc itself is a protective adaptation seems almost beyond question; but whether the annulations characteristic of this and many other hydroids is an additional adaptation, rendering the stem flexible, etc., may be doubtful.

VII. Abnormalities.

The eccentric forms of cleavage already considered naturally raise the question as to probabilities of corresponding anomalies among the larvæ of these forms, and also of the resulting polyps; whether at any rate any variation appears from the normal type of embryo. The answer in part may be inferred from a glance at Pl. I, Figs. 4–6. These represent but three out of a considerable number of eccentric forms observed during the progress of the work. As will be seen, Fig. 4 represents what might be designated as a twin planula, having a rather broad and blunt anterior and a bifurcated posterior. In Fig. 5 is represented a second type, quite common, which differs from the former chiefly in the shape of the body of the embryo, which is somewhat spindle-shaped, and also in the slender and attenuated character of the posterior bifurcated portions. In Fig. 8 is shown a third type which is somewhat unusual. The body portion is decidedly eccentric in shape, with irregular tentaculate processes arising from it at various points and of various sizes and shapes.

Whether such anomalies occur to any extent under perfectly natural conditions, of course, cannot be said. But from their occurrence under the most favorable conditions in aquaria, and since, moreover, they seemed in no way to interfere with subse-

quent development, it may be inferred that their occurrence in a state of nature is not in the least improbable. Similar abnormalities have been reported among other genera of hydroids, *e.g.*, Bunting ('94) figures embryos of very similar character. Now whether all such anomalous planulæ develop into normal polyp may not be easily determined. That many should not is only what constantly happens with the most typical. That some of them develop there is not the slightest doubt. In Fig. 6 is shown a specimen which had become fixed in the ordinary way and had developed tentacles upon apparently two polyps heads. And in this connection it may be noted that in many cases these anomalous processes have been seen to be resorbed into the body of the larva as it approaches the period of transformation. This may suggest that they are perhaps only temporary processes which may serve some temporary function of doubtful significance. The larva shown in Fig. 4 might suggest that it had its origin as a twin from a single egg which had segmented somewhat as represented in Pl. III, Fig. 4, where development of the two halves of the ovum had gone on so apparently independently. But in no specific case, several of which had been isolated and watched with care, had any such form resulted. Nor, further, in specimens of similar larvæ carefully sectioned was there any special evidence of such an origin.

I am rather disposed to consider them as due in all cases to the intrinsic prepotency of hydroids to bud and branch; for, as I have repeatedly observed, and as Pl. I, Fig. 8, will show, the budding propensity asserts itself very early in the polyp life.

Concerning abnormalities among adult hydroids of this genus I have made no extended observations. Bunting ('94) refers to several cases among Hydractinia and Podocoryne. But in these the polymorphic conditions would, it seems to me, render them specially favorable subjects in which to expect such divergencies, while in Pennaria, at least, this element is lacking.

In Fig. 1 of the text is shown a somewhat unusual, though possibly not abnormal, young polyp. As will be noted, its unusual feature consists chiefly in the total annulation of the

stem, including the branch. This is in rather striking contrast with those figured in the plates and in the well-known annulations of the stems of the Pennaridæ. I was for a time constrained to wonder whether this might not have been a specimen of some other genus which had accidentally been brought in with the collections and had developed along with the Pennaria. Such a supposition is not impossible of course, yet the general aspects of the hydroid are so peculiarly pennarian, the annulations excepted, that I am rather constrained to regard it as simply a specimen which exhibits, in an unusual degree, a phenomenon which in itself is one of the most variable among hydroid characters, and that it shows how unreliable must be such a character for diagnostic purposes.

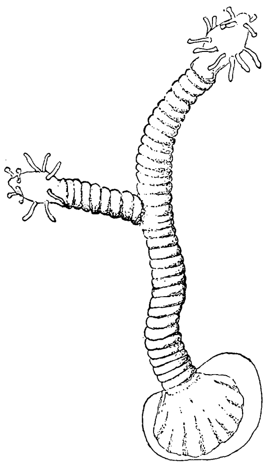

FIG. 1.

VIII. EXPERIMENTAL.

1. *Darkness.* — The liberation of the medusæ and the discharge of the sexual products upon the approach of darkness suggested this as a possible cause of the unusual activity at this time. Accordingly, several experiments were made to determine whether such were really the case. Colonies of both sexes were collected about 3 P.M. and were carefully excluded from light in suitable receptacles, but in no case could they be induced to discharge their products or become free at an earlier time, though that such conditions might have at some time in the life of the race been a factor in determining the periodicity of their maturity and release may not be improbable. But, as has already been pointed out, the fact that the deeper water forms do not become free or discharge the sexual products until toward midnight would certainly seem to suggest that darkness alone could not be the determining factor.

2. *Temperature.* — The observation that during specially warm weather larger numbers were liberated suggested the

possible influence of temperature upon the maturity of the medusæ, and suggested also additional experiments. Artificial change of temperature by means of heat or ice had a very noticeable effect, both upon the activity of the medusæ and the cleavage of the eggs, the reduction of temperature by a few degrees materially retarding the rate of cleavage, while raising it a corresponding amount proportionately accelerated these phenomena. This was likewise evident in the development and activity of the larvæ.

3. *Artificial Division of the Eggs.* — During the earlier phases of segmentation experiments were made to determine the effects of detaching small portions of the egg, in imitation of the observed spontaneous detachment of particles from the surface, to which reference has already been made. From repeated experiments it was conclusively shown that removal of small portions, and indeed of considerable portions, did not materially retard or modify the development of the eggs, or prevent their final development into perfect larvæ.

Again, the experiment of dividing eggs at the first cleavage, and at the second, and also of dividing them into several portions, was made in a considerable number of cases, with the results of obtaining from these fractions perfectly normal, though small, embryos, which continued to thrive and, finally, in the usual time transformed into perfectly normal polyps. Pl. III, Fig. 11, shows one of these half-egg polyps which was isolated and reared under conditions which leave no shadow of doubt as to the genuineness of the case. And this is only one of a considerable number, some from smaller portions, which were similarly secured. In Fig. 2 of text are shown a series of planulæ of normal and artificially produced specimens, in which the relative sizes are clearly exhibited.

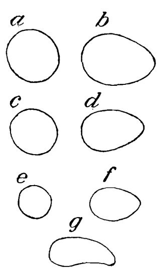

Fig. 2.

On a preceding page attention was directed to a rather remarkable feature, namely, the natural origin of two embryos from a single egg, by a spontaneous division at some point during the segmentation. These facts would seem to show conclusively that so far as the hydroids are concerned there is no such pre-

determined organization of the egg as that a given part must necessarily determine a given organ or part. For in the half or fourth embryos the number of tentacles arising in the polyp was of the same number and arrangement as in the normal one.

So, too, in the formation of perisarc, rate of growth, etc., there was nothing to indicate that the larva was other than a normal one in every respect, that of size alone excepted.

It may not be without the range of these facts to refer in passing to similar experimental work by Driesch, Wilson, Loeb, and others and to refer in particular to that which is in some respects rather unique. Concerning the capacity of portions of eggs regularly to develop into perfect embryos it is unnecessary to make special mention at this time. Loeb has shown ('93) that under the unusual stress of osmosis, induced by varying the density of the medium, double or multiple embryos of sea urchins might be produced almost at will. This has since been matter of common experiment. What seems to me of special note in connection with these experiments on Pennaria is that not only may such *experimental* results be obtained, but that similar results have been obtained in perfectly *normal* ways, that the entire phenomena of cleavage reproduce at some phase or other an almost identical counterpart of former experimentation along these lines. No one can follow the segmentation of the ova of Pennaria in its extremely variable and anomalous aspects without the conviction that there are here involved intrinsic forces, quite as pronounced as any which have been involved in the artificially operative chemical and physical agents to which reference has been made. That they may comprise much of chemistry and of physics is not questioned. But if so, they are intrinsic and integral.

SYRACUSE UNIVERSITY,
March 1, 1900.

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EXPLANATION OF PLATE I.

FIG. 1. Single colony of Pennaria, natural size, showing mode of typical branching, attachment to substratum, etc.

FIG. 2. Medusa about mature, showing form of ova at this stage, mode of attachment, etc.; *ov*, ova; *rc*, radial canals; *t*, tentacles.

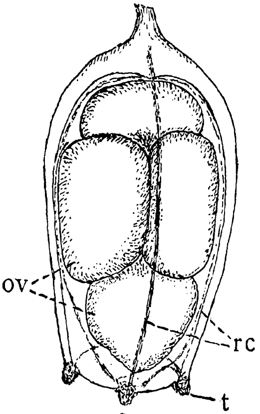
FIG. 3. Mature medusa, parts as in Fig. 2. Ova perfectly spherical, and clustered about the manubrium; *v*, velum.

FIGS. 4, 5. Abnormal larvæ, as found in several cases, showing the bifurcated condition.

FIG. 6. Rather unusual type of polyp, with small bud, *b*, on side of body, and with less than usual number of tentacles.

FIG. 7. Typical planula, about twenty-four hours after laying of the egg.

FIG. 8. An unusual larva, similar in some respects to that of polyp in Fig. 6, but with several bud-like developments, *b*, *b′*, *b″*.



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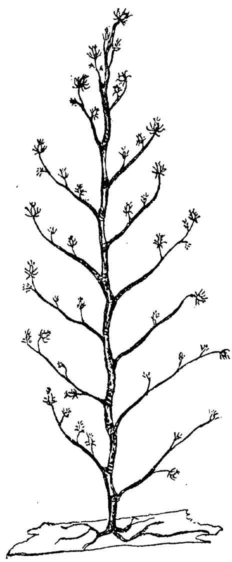
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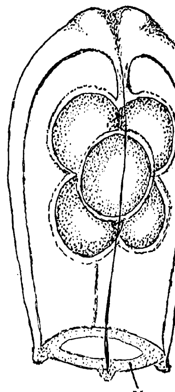

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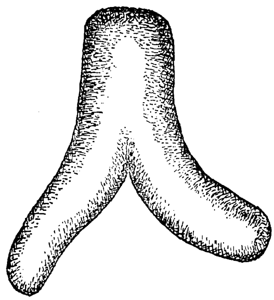
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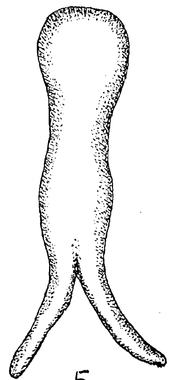
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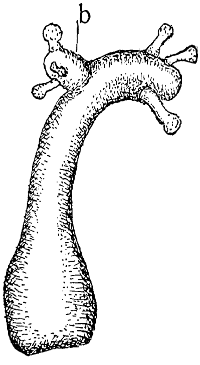

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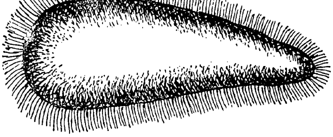
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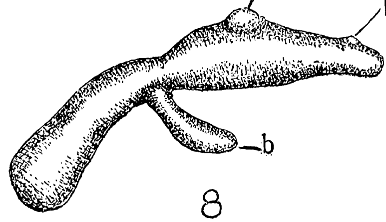

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EXPLANATION OF PLATE II.

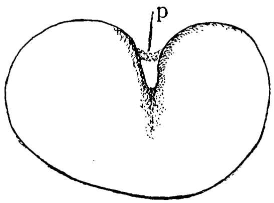
FIG. 1. Egg in first cleavage phase; *p*, a protoplasmic band connecting the blastomeres.

FIG. 2. A second phase of cleavage, indicated by furrow cutting off a small blastomere at *x*. Two protoplasmic strands are shown, one, *p*, the same as in Fig. 1.

FIG. 3. Next phase ten minutes later.

FIGS. 4–6. Show successive phases in progress of the development.

FIGS. 7–11. Show phases of cleavage in another egg, which differ in some respects from the former, yet resulting in practically same condition.



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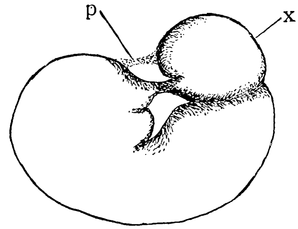

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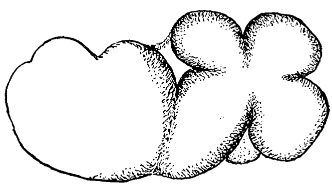

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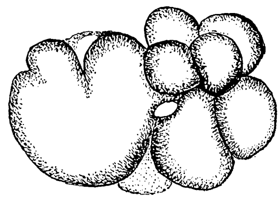

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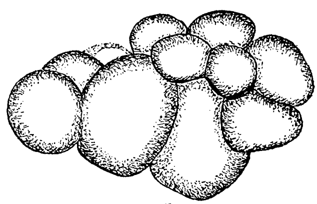

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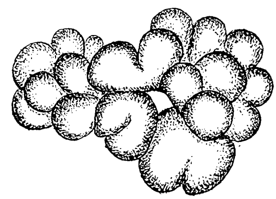

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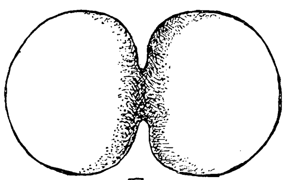

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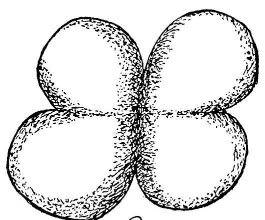

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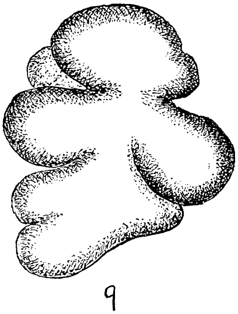

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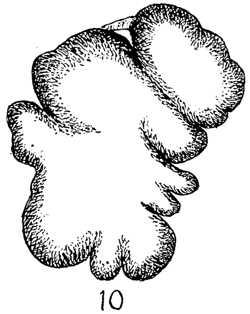

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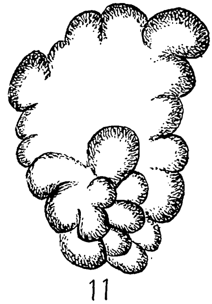

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EXPLANATION OF PLATE III.

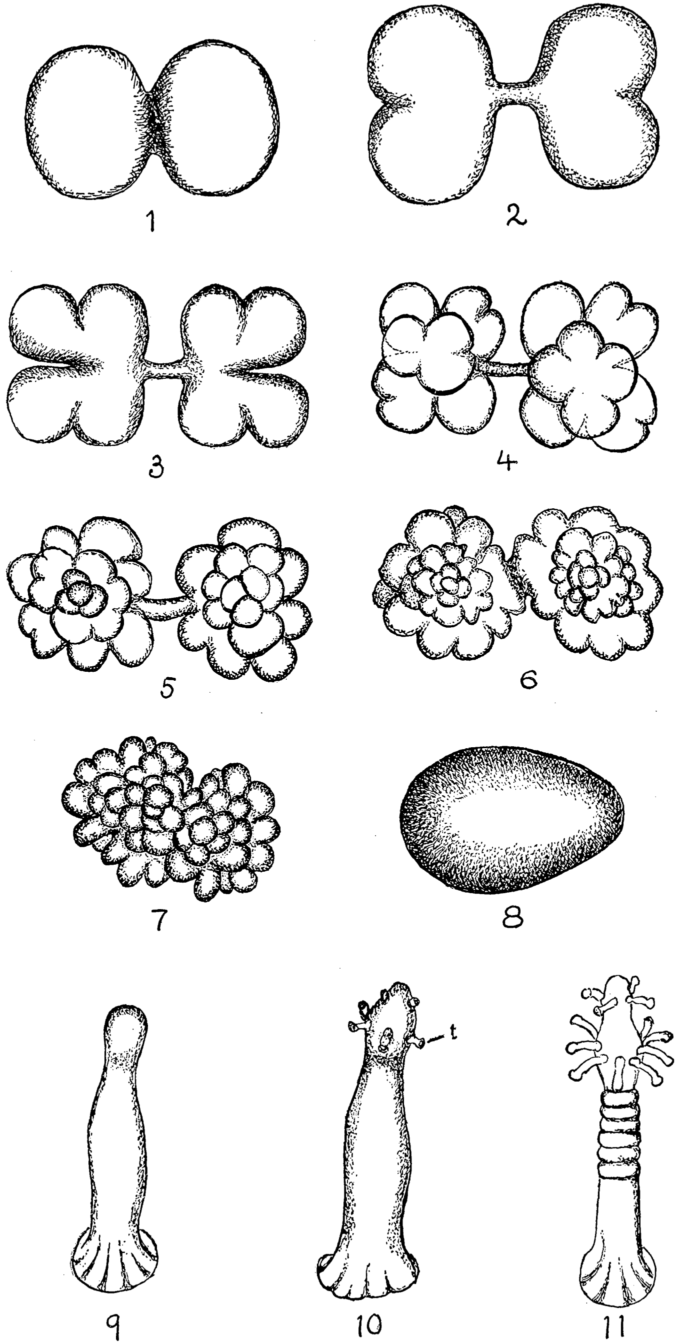
FIGS. 1–5. Show a phase of cleavage not uncommon, in which, after the first division, the blastomeres segment in a perfectly independent way.

FIGS. 6, 7. Show the final coalescence of the two portions, and in Fig. 8, the resulting morula, which gradually assumes the planula form of Fig. 7 of Pl. I. The figures of this series are somewhat diagrammatic.

FIG. 9. Young polyp phase soon after attachment.

FIG. 10. Polyp with budding tentacles, *t*.

FIG. 11. Fully grown polyp, with full complement of tentacles, mouth, annulation of perisarc, etc. Sketched from life, with camera.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EXPLANATION OF PLATE IV.

FIG. 1. Section of entire egg in early cleavage phase, showing more rapid rate at one pole, while the opposite shows a resting nucleus and no indications of segmentation. Camera sketch, × about 45.

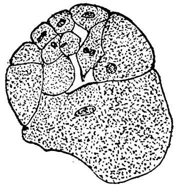
FIG. 2. Two-cell stage. At the left is shown a perfect nuclear spindle, *sp*, and in the opposite blastomere several asters, which may indicate the nuclear divisions which have occurred, without involving the cytoplasm.

FIG. 3. Section of egg, × 135, showing various internal cleavage conditions, chiefly superficial; *n*, nuclei in resting condition.

FIG. 4. Portion of egg more highly magnified.

FIG. 5. Portion of another egg, showing essentially similar conditions.

FIG. 6. Section of egg at completion of segmentation, showing a mass of nuclei partially organized into a cellular ectoderm, *ec*.



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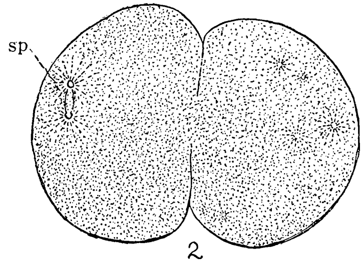

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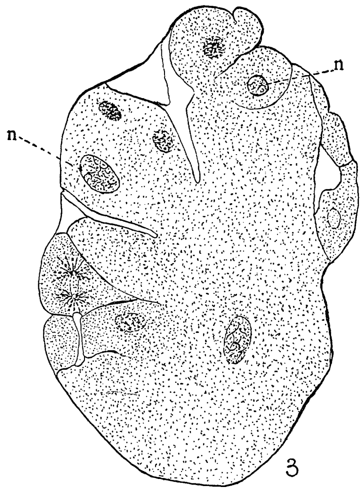

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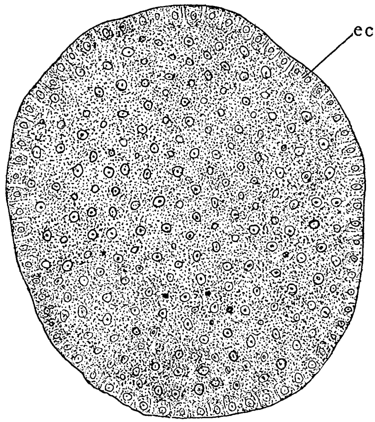

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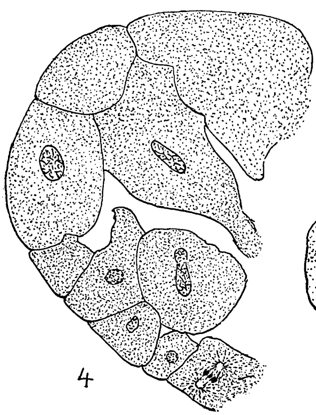

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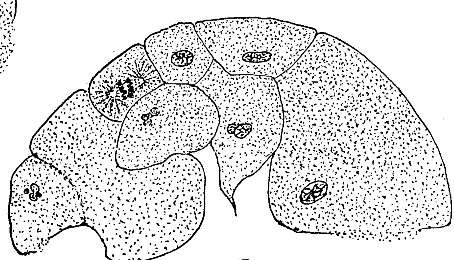

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